



Short communication

Ecotourism increases the field metabolic rate of whitetip reef sharks

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ABSTRACT

Wildlife tourism has been shown to cause behavioural changes to numerous species. Yet, there is still little understanding if behavioural changes have consequences for health and fitness. The current study combined accelerometry and respirometry to show that provisioning whitetip reef sharks (*Triaenodon obesus*) for tourism increases their daily energy expenditure by elevating activity levels during periods when they normally rest. Field metabolic rate increased by 6.37% on provisioning days compared to non-provisioning days. Since metabolism is a key parameter influencing most biological and ecological processes, this represents some of the clearest evidence to date that ecotourism can impact critical biological functions in wild animals.

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1. Introduction

There is a growing body of work investigating the impacts of wildlife tourism on animals. Changes in behaviour have been documented for several species that are regularly subjected to wildlife tourism (Orams, 2002; Burgin and Hardiman, 2015). However, behavioural information alone may not be sufficient to fully understand impacts of wildlife tourism, as changes in behaviour do not necessarily indicate changes in health or fitness (Gill et al., 2001; Beale and Monaghan, 2004). Studies that quantify physiological parameters can contribute to a better understanding of whether ecotourism impacts animal health and fitness (e.g. Semeniuk et al., 2009; French et al., 2011), but the overall lack of information on physiological impacts is a reoccurring issue across most groups of animals involved in wildlife tourism.

Provisioning and/or using an attractant to concentrate animals for reliable viewing are forms of wildlife tourism that can have particularly strong impacts on animal behaviour. Effects range from minor short-term alterations of behaviour (e.g. short-term interest in provisioning or avoidance behaviour), to long-term modifications of abundance and conditioning to feeding events (Orams, 2002; Burgin and

Hardiman, 2015). Elasmobranchs (sharks and rays) are a group in which provisioning-induced behavioural changes have been most commonly documented, and while possible fitness issues have been acknowledged (Gallagher et al., 2015), the only study that found definite evidence of negative impacts on an elasmobranch's health/fitness was at the Grand Cayman Island provisioning operation of southern stingrays *Dasyatis americana* (Semeniuk et al., 2009).

Metabolism is crucial to all biological and ecological processes, and the rates at which animals acquire and expend energy have direct and fundamental consequences for their survival and fitness (Brown et al., 2004). Quantifying key processes such as activity level, metabolic rate and food intake provides important information for determining the allocation of energy to crucial activities such as growth and reproduction. Accelerometry has emerged as a useful method for quantifying energy expenditure via the measurement of dynamic body acceleration, which can then be used as a proxy for estimating metabolic rates in the wild (Wilson et al., 2006; Payne et al., 2011).

Whitetip reef sharks *Triaenodon obesus* (Ruppell 1837) are regularly provisioned at an isolated seamount, Osprey Reef, Australia. Previous work at Osprey Reef and captive studies suggest *T. obesus* are nocturnally active and rest during the day (Whitney et al., 2007; Fitzpatrick et al., 2011). However, vertical activity during the day increased significantly on days in which shark provisioning occurred (Fitzpatrick et al., 2011). Human induced behavioural changes like this could impact the energy budgets of sharks exposed to provisioning, but no previous studies

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have provided a quantitative estimate of the effects of tourism on the metabolic rates of sharks in the wild. In light of the findings in Fitzpatrick et al. (2011) and the ever increasing popularity of shark provisioning, there is a clear need for this highly relevant issue to be addressed in more detail. This study combines measurements of metabolic rates in the laboratory with accelerometry in the wild to investigate the impact of provisioning tourism on the energetics of *T. obesus*.

2. Methods

2.1. Respirometry experiments

Respirometry experiments were conducted at Cairns Marine, Cairns, Australia cairnsmarine.com. Trials were run indoors between 8:00–17:00. Metabolic rates (oxygen consumption rates in $\text{mg O}_2 \text{ h}^{-1}$; calculated from the rate of decline in oxygen concentration in respirometers) during resting and swimming were measured in five *T. obesus* (total length (TL) range: 76–105 cm, mass range: 2.0–6.0 kg, juvenile-sub-adult). Initially we attempted to swim *T. obesus* at a variety of speeds in a 690 L swim-tunnel respirometer (dimensions: 40 cm diameter \times 120 cm length), but given their negative buoyancy, ability to buccal pump and propensity to rest on the seafloor, swimming could not be induced, so only resting metabolic rates were measured in the swim-tunnel. Each shark was acclimated to the swim-tunnel for approximately 2 h before dissolved oxygen concentrations were measured, with readings from the last 10–20-min used to calculate oxygen consumption rates. To measure metabolic rates during swimming, the same individual sharks were placed in a larger (17,920 L) holding tank and sealed with plastic sheeting, which saw them swim continuously for several hours. A water pump was fixed to the bottom of the (17,920 L) holding tank respirometer to maintain gentle centrifugal flow, and given sharks swam continuously, we considered oxygen to be well-mixed during each trial. Since the tank was circular, and turning can cause higher energy expenditure (Krohn and Boisclair, 1993; Wilson et al., 2015), the measure of active metabolic rate could be an overestimate. For both swim-tunnel and large respirometer trials, oxygen concentration and water temperature were monitored with an LDO101 model dissolved oxygen probe and HQ40d multi-parameter meter (Hach™; Loveland, USA). The probe was fixed within a small (~100 mL) sealed sump outside the swim-tunnel or large respirometer, with water drawn from the respirometers by a small aquarium pump and hose, and returned via another hose. The probe had a sampling frequency of 0.1 Hz, a manufacturer-reported accuracy of 0.1 mg L^{-1} , and was calibrated to 100% oxygen saturation in air prior to swim trials (see Payne et al., 2015 for details of experimental set up). Trials in the large respirometer lasted 2 h, with the last ~60 min used to calculate the rate of decline in dissolved oxygen. Individual sharks were used once for swim tunnel and large respirometer trials. Throughout all trials, water temperature remained at $27.0 \pm 0.5 \text{ }^\circ\text{C}$, and oxygen concentrations above 80% saturation (assuming 6.6 mg L^{-1} in saturated seawater). A 1 h control run was carried out after the last respirometry measurement for empty (no shark) swim-tunnel and large respirometer, and any background respiration rate was subtracted from the animal measurements.

2.2. Field study

The study site, North Horn is located on the northern tip of Osprey Reef ($13^\circ 54.190'\text{S}$, $146^\circ 38.985'\text{E}$). Fieldwork was conducted over 16 days (28th November to 13th of December 2009), and during this time three dive operators conducted a total of seven provisioning events on five different days (between 10:00 and 16:50), each lasting approximately 1 h. See Fitzpatrick et al. (2011) for details of North Horn and shark provisioning activities. *Triaenodon obesus* show strong residency to North Horn. North Horn is a core resting area during the day, with

sharks dispersing 3–5 km during the night. So, eight VR2w acoustic receivers (VEMCO Ltd., Halifax, Canada) were deployed within 3 km of North Horn (500–660 m apart) to monitor tagged sharks in their core habitat (Barnett et al., 2012). Range testing of receivers showed that the distance at which 100% of transmissions were recorded was 400 m (Barnett et al., 2012).

Eight adult female *T. obesus* (125–145 cm) were externally tagged with bi-axial accelerometer acoustic transmitters (see Fitzpatrick et al., 2011 for capture methods), model V9AP-2L, 69 kHz, 3.3 g in water, and 66 mm length (Vemco, Halifax, Nova Scotia). Using corrodible wire encased in a plastic tube, transmitters were secured to the caudal peduncle with the length of the transmitter (the longest dimension of the cylindrical transmitter) parallel to animal length, so they recorded acceleration in the X (side to side) and Z (up and down) axes. Acceleration and depth data were transmitted at random intervals between 50 and 130 s. Acceleration ($\pm 29.4 \text{ m s}^{-2}$ range) was sampled at 10 Hz for 17–40 s every second transmission cycle (24% duty cycle). Acceleration was calculated as an average root mean square (RMS) value for both axes (acceleration = $[\text{X}^2 + \text{Z}^2]^{0.5}$) each 17–40 s period and transmitted as an 8 bit digital value. The acceleration value is also termed body activity/acceleration. The static contribution to overall g was filtered out prior to RMS calculation. RMS acceleration resolution was 0.0191 m s^{-2} (Payne et al., 2011).

2.3. Statistical analyses

Analysis was conducted in R. Linear regression analysis was used to investigate the relationship between oxygen concentrations and time in both tank trials. Resting and swimming metabolic rates were estimated for all individual sharks ($\text{mg O}_2 \text{ h}^{-1}$), and scaled for mass-specific metabolic rates (Clarke and Johnston, 1999; Payne et al., 2015).

Linear mixed-models were used to test whether provisioning influenced body activity levels of *T. obesus*, with time of day (day vs. night; categorised according to the timing of local sunrise and sunset) and provisioning (days in which provisioning did or did not occur) treated as fixed effects and shark ID as random. A first-order correlation structure was included in the models to account for serial autocorrelation (a violation of the assumption of independence in model-fitting) (Payne et al., 2012). We were interested in whether any influence of provisioning on body activity varied between day and night, so included the interaction term in our model (time of day \times provisioning). Alpha was set at 0.05.

Because metabolic rates could only be measured in the laboratory at two activity levels (resting and preferred swimming speed) we could not generate a reliable calibration relationship between body acceleration and metabolic rate to estimate field energetics as others have done (e.g. Wilson et al., 2006; Payne et al., 2011). However, since wild *T. obesus* spend a high proportion of time motionless on the seafloor, we expected their distribution of body activity levels to be strongly bimodal, such that our accelerometers could readily enable us to quantify the proportion of time that sharks were “resting” versus “swimming” in the wild. Since respirometry experiments revealed the energetic costs of resting and swimming at preferred speeds, we adopted a binary approach to estimating field metabolic rates in *T. obesus*, based on the measured energetic costs of resting and swimming. We acknowledge that this approach may under- or over-estimate field metabolic rates to some degree, but nevertheless this method accounts for several of the major sources of uncertainty in field energetics: time spent active and species-specific metabolic rates at different body activity levels.

To estimate field metabolic rate, we assigned all field body activity data to two categories: provisioning days (the 24 h periods in which provisioning events took place) and non-provisioning days. We then created frequency distributions of field activity for these two categories, and examined the bimodal distributions of the data to estimate the proportion of time spent “resting” and “swimming” during both provisioning and non-provisioning days. Laboratory metabolic rate measurements during resting and swimming were then used to estimate daily energy

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